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Regional and Local Vegetation Patterns
The Responses of Vegetation to Subcontinental Air Masses

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REGIONAL AND LOCAL VEGETATION PATTERNS: THE RESPONSES OF VEGETATION TO SUBCONTINENTAL AIR MASSES

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Regional and Local Vegetation Patterns: The Responses of Vegetation to Subcontinental Air Masses

ABSTRACT

Spatial patterns of biodiversity in plants were examined through a range of scales from continental and biome to patterns of local habitat variation. We propose a hierarchy of constraints on these patterns. Large-scale climate is proposed to structure continental patterns of species richness (Currie and Paquin 1987) and the diversity and distribution of physiognomic types in the form of biomes. Within biomes regional climatic gradients modulate the length scales of habitats (i.e., grain size) and, hence, the amount of substrate variation within a grain that is 'perceived' by an organism as homogeneous. Most resource variation in the core of biomes is within a given species' range of tolerance and large areas of the landscape are 'perceived' as essentially homogeneous. As one moves toward ecotones, the convergence of regional climatic stresses constrains the suitability of habitats to smaller scale variations in substrate and topography. Thus, the size of habitat grain declines, while the diversity of habitat grains increases toward biome ecotones. Biotic interactions form a third level of constraint, operating at yet a smaller spatial scale, to further modify local species associations. These regional gradients in habitat size and variability provide explanatory power of observed patterns in biodiversity and provide a monitoring tool for climate-induced changes in ecotones.

INTRODUCTION

The prospect of global change, fostered by human impacts on the global climate and by extensive alteration of the natural landscape, has raised concerns over the fate of the Earth's natural biological diversity. Unfortunately, a definitive theory on the causes of biological diversity has been elusive. The absence of such a theory makes it difficult to project the consequences of global change on biodiversity as a resource. The ideal theory of biodiversity must, at least, be able to explain the spatial patterns of biodiversity and their changes through time. Our intent in this paper is to explore some of the spatial patterns of biodiversity and to propose a few mechanisms that appear to account for much of this pattern. We will be

particularly attentive to the potential climatic drivers of spatial patterns of biodiversity.

Diversity can be defined in many different ways. Two manifestations of diversity, 1) diversity of form, i.e., physiognomy, and 2) diversity of species will be addressed in this paper. Physiognomy refers to the outward features or appearance of an object. The term is useful, for example, in referring to forested as opposed to grassland biomes. Within a biome, physiognomy can refer to the vegetation structure, for example, the different relative amounts of overstory and understory life-forms. Species diversity has two components, richness and evenness (Cody 1975, Whittaker 1972). Species richness is the number of species in a sample; while, evenness refers to their relative abundances (Ibid.). Of these two components we will restrict our discussion to species richness.

Spatial patterns of both physiognomic and species diversity have resulted from processes on two vastly different time scales, evolutionary and ecological. Over evolutionary time, new species and life-forms arise, but this process usually requires millennia for terrestrial plants. Over ecological time, years to centuries, evolution can be assumed static and spatial patterns of species diversity arise from different spatial arrangements of species due to climatic and substrate forcing or ecological interactions. Evolutionary time frames and processes will not be discussed in this paper. Rather, we will attempt to extract the different influences of climate over short time scales on spatial patterns of diversity across a range of spatial scales. In addition to the separation of potential causes of diversity patterns at different scales, we will look for mechanistic relationships between climate at large spatial scales and patterns of diversity at large and small spatial scales.

Recent reports suggest that climatic change could cause biomes to shift several hundred kilometers across the Earth and that the physiognomy of any given biome could rapidly change to something quite different (e.g., Neilson et al. 1989, Neilson et al. 1990, Solomon 1986, Winjum and Neilson 1989). Both types of change, spatial and physiognomic, could threaten the extinction of large numbers of species. The ecotones between major biomes will likely be landscapes that are sensitive to climatic change (di Castri et al. 1988) and should possess patterns of biodiversity that are unique relative to more

central biome areas. We will first describe a theory of physiognomic diversity and spatial distribution as driven by large-scale climatic patterns. This theory should explain the general physiognomy within biomes, as well as the location of the ecotones between biomes. We will then attempt to relate local patterns of species diversity to the distributions of biomes with particular attention to the relationships between diversity patterns and ecotones at regional and local scales.

BIOMES AND ECOTONES - CLIMATE

Consider the distribution of biomes and associated species within the conterminous United States (Fig. 1; Dice 1943, Küchler 1964). These homogeneous biomes exist by virtue of relatively homogeneous climatic regions, dispersed over the continent. Continental climatic patterns are produced by the passage of particular synoptic weather types, such as cold-lows, over a specific region with particular seasonal frequencies (Bryson and Hare 1974, Horn and Bryson 1960, Manabe and Broccoli 1990, Neilson et al. 1989, Wendland and Bryson 1981). The spatial extent of these regions is under control of the steering of weather systems by upper air wind patterns. The dominant upper-air jet streams are indicators of the spatial extent and seasonal positions of the different storm tracks and clear weather patterns. These wind patterns flow over the continents in relatively well known patterns and produce regions of climate that are fairly distinct from one another.

The spatial patterns of seasonal weather associated with these different climatic regions and biomes were analyzed by constructing a grid of line transects through a network of long-term weather stations over the conterminous United States (Neilson et al. 1989, Quinlan et al. 1987). Two transects from the grid illustrate most of the relevant climatic pattern (Figs. 1-3). The seasonality of rainfall is quite homogeneous at the geographic scale of biomes (Figs. 2, 3) and can be related to the large-scale circulation features and storm-tracks in the global atmosphere (Bryson and Hare 1974, Horn and Bryson 1960, Neilson and Wullstein 1983).

The eastern forested region averages high precipitation in all months of the year (Figs. 2, 3). The boundary of the eastern forested region with the Great Plains is accompanied in both transects (Figs. 2, 3) by a rather sharp decline in winter precipitation. Summer precipitation in the Great Plains is

high in the Tall Grass Prairie (Fig. 2), but low in the southern plains (Fig. 3). The near absence of winter rains and the presence of spring rains appear to be the primary climatic features determining the distribution of the Great Plains grasslands (Figs. 2, 3). Given these two conditions, variations in summer and fall rains appear to produce the sub-regional distributions of, for example, Short Grass Prairie in Colorado (Fig. 2) or mesquite-grassland in Texas (Fig. 3). The Great Basin Sagebrush-Steppe vegetation corresponds to a rise in winter precipitation (Fig. 2); while the southwest deserts correspond to a near absence of spring and fall rains, relatively dry winters and the presence or absence of summer rains (Fig. 3). West coast vegetation is typified by high winter rainfall and low summer rainfall (Figs. 2, 3). The northwest coast is separated from the southwest coast by a large gradient in winter rainfall (Figs. 2, 3), as well as temperature (data not shown; Neilson et al. 1989).

We suggest that these relationships are more than simply correlational, but are mechanistically rooted in the regional water balance and thermal regimes. Regional precipitation controls the input side of the regional water balance; while, 1) evapotranspiration (ET) from vegetation and soil surfaces and 2) runoff dominate the output side of the regional water balance (ignoring deep aquifer recharge). Regional comparisons between the spatial patterns of seasonal precipitation and runoff (Figs. 2, 4) allow an examination of two of the regional water balance terms, allowing inferences about evapotranspiration and, hence, vegetation relationships to climate.[1]

Surface runoff delineates the major biome boundaries even more succinctly than the climatic patterns (Fig. 4). The prairie - forest ecotone, for example, corresponds to a change from runoff all year in the forested region to only spring runoff in the prairie. The only biomes in the country that exhibit significant summer runoff are those that receive sufficient winter precipitation to recharge a deep soil reservoir of water (Fig. 4). The amount of deep soil recharge appears to just compensate for withdrawal by deeply rooted woody plants during the growing season (e.g., compare figures 2

[1]Continental scale runoff patterns were examined with a similar transect approach based on USGS stream gauge data (US West 1988) from watersheds of 100-200 km^2 drainage area.

and 4; Neilson et al. 1989, Stephenson 1990). There appear to be no broad areas in the conterminous U.S. where the summer rainfall is sufficient to balance the demand for evapotranspiration (ET). The size of the deep soil reservoir appears to select for a specific leaf area and biomass that can be supported by the ET, thus defining the boundaries between forest and grassland biomes and between grassland and shrubland (Neilson et al. 1989, Stephenson 1990, Woodward 1987). The grassland vegetation of the continent is sensitive to near-surface soil moisture and appears to be directly coupled to spring soil moisture and spring rains with summer rains allowing greater biomass and, perhaps, more species. Woody vegetation relies on near-surface soil moisture for establishment, but thereafter is less strongly coupled to growing season rainfall. The woody vegetation appears to be strongly coupled to winter precipitation and its subsequent recharge of deep soil moisture.

Direct effects of cold temperatures appear to control some boundaries while water balance appears to control the life-form within the boundaries (Neilson et al. 1989). The anucleate freezing point of super-cooled water, ca. -40°C, appears to control the northern boundary of the eastern deciduous forest with the boreal forest (Burke et al. 1976). The nucleate freezing point of water at 0°C appears to control the northern boundary of the southeast pines and hardwoods in the U.S., the boundary between the Sonoran and Chihuahuan deserts, and interacts with drought to control northern boundaries of oaks, pinyons and junipers in the Rocky Mountains and the Great Basin (Neilson 1987a, Neilson 1987b, Neilson and Wullstein 1983, Neilson et al. 1989, Stephenson 1990).

In conclusion, biome-scale patterns of physiognomic diversity appear to be largely controlled by the regional water balance and in some cases cold winter temperatures. Currie and Paquin (1987, and *personal communication*) suggest that species richness at the biome and continental scales is also largely controlled by the regional water balance, although the potential mechanism is not clear.

REGIONAL CLIMATIC GRADIENTS AND LOCAL HABITAT SCALING

The regionalization of climate provides the first level of constraint that produces a biome type. Within any biome will be variations of substrate,

topographic and edaphic, that produce local patterns of community variation. Variations in the physical geography and substrate clearly occur through a range of length scales from local rill and gully microtopography to regional mountain axes. In any given landscape there will be a length scale above which plants of a particular size 'view' substrate variability as heterogeneous and below which substrate variability is 'viewed' as homogeneous or of little importance to survival. This length scale determines the relative 'grain' size of the environment as 'perceived' by the organism (Levins 1968).

The size of a homogeneous grain is defined by the physical mapping of the tolerable range of an organism's resource gradient onto the physical geography or substrate containing the resource (Levins 1968, Whittaker et al. 1973). This is a critical definition in that variations in habitat that fall within the tolerable resource gradient are not resolved and simply comprise a part of a homogeneous grain. For example, in landscapes where a species occupies both north and south facing slopes, the grain is quite large; while, in areas where a species is restricted to either a north or a south facing slope, the grain is correspondingly smaller. These arguments refer only to the presence or absence of a species and not its abundance or productivity.

Regional climatic gradients appear to modulate the grain size of the environment as 'perceived' by the organism. In short, if the regional climate is not overly stressful (as in the core of a biome), then the range of available substrates for an organism will fall well within the tolerable resource gradient with a spatial scale of large extent, possibly kilometers (Fig. 5; Axelrod 1967, Neilson and Wullstein 1983, Stebbins 1952). However, if the regional climate is marginal (near the periphery of biomes), many local variations in topography could place some microhabitats outside the range of tolerance (Fig. 5; Ibid.). An example will help illustrate these points.

The upper elevational boundaries of plant species' distributions in the central Rocky Mountains tend to be controlled by cold temperatures and, thus, rise in elevation with decreasing latitude (Fig. 6; Neilson and Wullstein 1983). The lower bounds of species distributions in the central Rocky Mountains tend to be controlled by the amount of growing season rainfall which increases to the south (the Arizona Monsoon, Bryson and Lowry 1955). Thus, the lower elevational bounds decrease with decreasing latitude, opposite to

the temperature gradient (Fig. 6). Transplant studies of over 700 tree seedlings throughout the region indicated that where the regional climate was not stressful, the seedlings survived equally well on all aspects and elevations and under different levels of cover (Neilson and Wullstein 1983, Neilson and Wullstein 1986). Minor variations in substrate were within the range of tolerance and the habitat grain was quite large.

However, as the temperature and rainfall constraints converged in elevation at the northern boundary of the species, seedling survivorship was more and more constrained to specific slopes, elevations and cover characteristics. Those microhabitats outside the range of tolerance of the 'target' species were occupied by physiologically or ecologically different species, often from the neighboring biome. Thus, a comparatively larger proportion of the local physical habitat variability was physiologically tolerable in the core region than near the boundary. Near ecotones, habitat grain becomes smaller and more varied. The small size and high variability of habitats near ecotones can be viewed as an interfingering of neighboring climates as well as an interfingering of neighboring biomes.

Is the model of regional control of habitat size and variation a general model? In the example of the central Rocky Mountains the single requirement for the model was that regional temperature and rainfall gradients were not parallel (Neilson and Wullstein 1983). We propose that this condition is ubiquitous for the biome ecotones of North America and likely throughout the world.

Although seasonal temperatures decrease monotonically toward the pole, rainfall amounts exhibit maxima and minima with increasing latitude (Neilson et al. 1989). Therefore, along any north-south transect across a biome ecotone, the temperature and rainfall gradients will not be parallel. Similarly, the longitudinal transects at the continental scale (Figs. 2, 3) are remarkable for the variations in rainfall, less so for temperature (data not shown, Ibid.). Again, the two stressors do not produce parallel gradients. The coincidence of a steep gradient in either rainfall or temperature with known ecotones will be reflected by some form of 'wedge' of tolerable environments (as in Figure 6).

HABITAT SCALING AND SPECIES INTERACTIONS

When the size of a homogeneous grain is large relative to the individual, as in a core region, it can be occupied by many different individuals and species with overlapping limits of tolerance. Competition among individuals in this case will be diffuse. In satellite regions, where the size of individual homogeneous grains could be on the order of that of a single individual, only one or a few individuals might occupy any given grain. Competition between individuals of the same species and between ecologically very similar species will become quite strong. Thus, the change in grain structure along regional climatic gradients should be common and should modulate the kind and intensity of competition among organisms (Neilson and Wullstein 1986, Watson 1980). In the Rocky Mountains, such re-scaling of the habitat results in species specific competition near range limits and diffuse competition in more central locations (Neilson and Wullstein 1983, Neilson and Wullstein 1986, Peet 1978).

What are the relationships between regional climatic gradients, habitat scaling and biodiversity? Regional or gamma diversity[2] patterns appear to be under the control of regional evapotranspiration patterns, a direct relation to large-scale climate, and topographic variability (Currie and Paquin 1987, and *personal communication*). Since gamma diversity is the sum of all species over a set of small plots, it will also be constrained by local or alpha diversity and beta or gradient diversity. Alpha diversity might be relatively high in the core region, where diffuse competition dominates and competitive exclusion would be less likely. Alpha diversity might be comparatively lower in ecotonal regions, as the patch size approaches that of the individual, and ecologically similar species might face more direct competitive exclusion.[3] In the latter case the stringent environment constrains the existence of only a few species to each homogeneous grain (Figs. 6, 7). Beta diversity, the rate of species turnover along a gradient, should increase toward the ecotone.

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[2]Species richness at large spatial scales is referred to as gamma diversity, while that at local scales is termed alpha diversity (Cody 1975, Whittaker 1972). The rate of change of species composition along a gradient is termed beta diversity (Ibid.).

[3]This statement assumes that alpha diversity is measured at a scale no larger than the grain size 'perceived' by the organism.

Adjacent plots along a substrate gradient in the core of a biome may show little change in community composition, since the entire gradient would be contained within a single grain. However, the same sampling structure repeated near an ecotone would traverse multiple small grains and indicate a high species turnover, i.e., beta diversity (see Delcourt and Delcourt 1990). From this analysis, gamma and alpha diversity metrics would not necessarily exhibit a pattern relative to ecotones even though the species identities would clearly be changing across the ecotone. For example, there may be ten species of plants on either side of an ecotone, but no species in common. Nevertheless, broad-scale patterns of gamma diversity should bear a coarse relation to the distributions of biomes and ecotones, since both appear to be heavily influenced by the regional water balance. Continental maps of species richness within different taxa appear to support this contention (e.g., Simpson 1964, Kiester 1971, Currie and Paquin 1987).

The manifestation of the 'wedge' of stressors will be quite different in a region with a homogeneous physical substrate (Fig. 6, 7). Under conditions where there is little physical variation in the environment, there are very few physical scale lengths upon which organisms can associate spatial resource variation. Gamma (regional) diversity and alpha (local) diversity could both be high in the core regions simply because the one substrate falls well within the physiological tolerances of many different species. Many species could coexist simply because of spatial separation, random dispersal and a general lack of a limiting climate. However, as one moves closer to the ecotone, the homogeneous substrate would become increasingly constrained by the climatic 'wedge' to the tolerance range of a single (or a few) species. Beta diversity would decrease from low to lower levels as would gamma and alpha diversity (Fig. 7).

Interestingly, the implication for the size of the patch in such a 'flatland' is that it is infinitely large in both core and satellite regions, but that it will support fewer species at the margins of the biome. In a physically heterogeneous region the resource variation within a grain should change very little, but the size and variety of grains should change considerably along core to ecotone transects. However, in a homogeneous region, the size and diversity of habitat grains should change very little, but the range of resource variation within the grain should be reduced near

the ecotone (Figs. 5, 7).

HABITAT VARIABILITY THROUGH TIME

The discussion to this point has focused on the regional, climatic control of local habitat diversity patterns over varying amounts of substrate diversity. We have seen that near biome boundaries, climatic constraints that limit physiognomic groups of organisms tend to converge. This produces regional gradients in the size or scale of suitable habitats or grains and, hence, the diversity of habitat grains within a landscape.

Through time these boundaries or ecotones move through space with shifting climate. The 'wedge' of environmental constraints (Fig. 6) will shift one direction or another and different grains in a landscape will alternately segregate and coalesce. Thus, any given landscape will be subjected to alternating periods of small and large habitat grain structure and, hence, high and low habitat diversity and direct versus diffuse competition. Each episode will, of course, promote its own unique pattern of biodiversity. However, the longevity of some organisms will induce a 'biological inertia' that will carry them as relicts into the next episode, adding an additional component to the overall landscape biodiversity (Neilson 1986). If the regional climate shifts back and forth with a high enough frequency, these long-lived organisms should become established or reestablished under one climatic regime while surviving in a nonreproductive state in subsequent climatic regimes, only to regain establishment as the climate swings back. These high frequency shifts in climatic regimes will clearly be more prevalent near already marginal areas, such as ecotones (Neilson 1986). These processes should contribute to higher diversity patterns in the vicinity of ecotones. The juxtaposition of such a time-varying landscape with high substrate variability will allow the expression of considerable biodiversity both in terms of species assemblages and species evolution (Axelrod 1967, Neilson and Wullstein 1983, Stebbins 1952).

TIME AND SPACE SCALES OF ORGANISMS

Local and regional patterns of biodiversity are further complicated by the diversity of different time and space scales of importance to organisms. Natural communities are composed of organisms that 'view' the environment over

a vast range of time and space scales. A small habitat grain to one organism, say a tree, may be a large grain to another, such as a soil microorganism (see e.g., Rusek 1990). This multiple scaling of organisms in communities, when placed in the context of the scaling rules just discussed, will produce a quite complicated assemblage of local and regional ecological communities. Thus, the measure of alpha (local) diversity is, in itself, scale dependent, with an appropriate sampling scale being quite different for trees as opposed to soil microorganisms (Rusek 1990).

Organisms, of course, intrinsically scale time as well as space. There are several critical time windows in life cycles, e.g., 1) the time required to produce a propagule (fertilization and development), 2) the time for dispersal and establishment, 3) the time to first reproduction, and 4) the length of the reproductive period. These can be telescoped into a very short time frame, as with annuals or some insects; or, they may be spread over long periods of time, as with long-lived trees. In the former case, all stages in the life cycle are sensitive to short term variations in weather. However, in the latter case, the early stages in the life cycle are critically sensitive to short-term variations in weather, but once established are more controlled by the long-term variations in weather.

Often the differential scaling of weather variation in time during different life history stages is accompanied by a differential scaling of substrate variation in space. For example, seedlings 'perceive' a spatial scale that is quite small compared to large adult trees and are sensitive to high frequency variations in weather. By contrast, even the spatial scale of large adult trees is swamped by the scale of large clones such as aspen or oak which can range over several hectares and can live for thousands of years through quite variable climates (Neilson and Wullstein 1983). The measures of alpha, beta, and gamma diversity are complicated by the intrinsic differences among the spatial scales of different species and the different life-history stages within a species. Interference patterns among organisms of different scales can also modify the local or alpha diversity patterns.

This organismal scaling of time and space is further complicated by the fact that the regional climatic gradients can modulate the expression of the phenotype within a life history stage, such that the organism may shift its scale of 'perception'. For example, in the case of Gambel oak (Quercus

gambelii Nutt.), the adult tree exists as a single stemmed individual or small clone in the southern part of its range, but as a very large clone in the northern part of its range (Neilson and Wullstein 1983). In this case the 'perceived' grain size for the adult remains quite large from the core to the northern boundary of the range; while, that for the seedling declines toward the northern boundary. In the case of the adult the 'perceived' grain size is much larger than a single individual in the south and any given grain is occupied by many different tree species. In the north the size of the grain is also very large, but so too is that of the individual clone. The number of species that can coexist in the ecotonal landscape is much reduced through a convergence of the tolerable limits of the habitat, the large grain size 'perceived' by the clone, and through intense competition with ecologically similar species. This is quite analogous to a homogeneous substrate as previously discussed, even though this occurs in a topographically diverse region, the Rocky Mountains.

The space and time scales of organisms combine in the context of geographic mobility and the 'inertia' of species' distributions. The longevity of organisms will determine the spatial lag in a trailing edge of a shifting biogeographic boundary and can be quite long, with spatial lags on the order of hundreds of kilometers and a persistence of thousands of years (Neilson and Wullstein 1983). Advancing geographic boundaries will be constrained in time by the potential rate of movement of propagules across a landscape, i.e., the dispersal distance and the age to first reproduction. If the rate of lateral climatic shifts exceeds the rate of dispersal, there will be a lag effect that will influence the local biodiversity patterns.

The overstory component of a community may be quite stable over time, because of the longevity of the trees or shrubs (biological inertia). However, shorter lived organisms within the canopy could change considerably from year to year or decade to decade with shifts in weather patterns (Neilson 1986). Attempts to relate today's diversity to today's weather may be inappropriate. Such relations between pattern and process could be further complicated by the amount of time that it might take for soils in the new region to adjust to the new climate in terms of physical and biological properties, potentially imparting yet another lag in biogeographic responses over space and time.

CONCLUSIONS - PATTERNS AND CONSTRAINTS

Spatial patterns of diversity present different kinds of information and suggest different kinds of drivers across a range of spatial scales. The most obvious feature of diversity at very large scales is the diversity of physiognomies. The physiognomy of a biome, the assemblage of different life-forms, can be readily related to large-scale patterns of climate and also to important ecosystem processes or functions, such as carbon or nutrient flows. The numbers of species, however, are less readily related to either climate or ecosystem processes. These points were aptly demonstrated in a series of classic studies comparing different biomes between the northern and southern hemispheres (Mooney 1977). The physiognomic classification of biomes was quite convergent under parallel climates; whereas, the numbers of species were highly variable when compared between the parallel physiognomies. The conclusion from these studies was that climate is the primary driver of physiognomic diversity, but that species diversity is more difficult to explain.

However, there are large-scale patterns of species diversity that do appear to be related to large-scale climatic features. There is, of course, a well-recognized latitudinal diversity gradient that likely bears some relation to global climate (Fischer 1960). Additional spatial patterns are revealed by continental-scale contour maps of species diversity within different taxonomic groups (e.g., Simpson 1964, Kiester 1971, Currie and Paquin 1987). These patterns bear a coarse resemblance to large-scale climatic regions. Furthermore, at continental scales, species richness within various taxa appears to bear a direct, linear relationship to the regional water balance (Currie and Paquin 1987, and *personal communication*). Thus, climate at regional to continental scales appears to be an important driver of both physiognomic diversity and species richness. Roughness of topography was the only other strong contributor to large-scale spatial patterns of diversity (Ibid.).

We propose that the constraints of climate, substrate and biotic interactions can be arrayed hierarchically, largely on the basis of their spatial or temporal extent of influence (Allen and Starr 1982, O'Neill et al. 1986). Global circulation patterns constrain the extent and timing of regional weather patterns. Regional weather gradients constrain core to

satellite patterns of habitat grain structure. The interference pattern of these exogenous, climatic constraints with a substrate of little or of great complexity will produce quite different manifestations of spatial diversity patterns.

The climate, substrate and biotic constraints are placed in this order because the climate remains homogeneous over a larger spatial extent than does the substrate, which is usually homogeneous over a larger spatial extent than individual organisms. Local variations in topography and substrate produce a variegated pattern of microclimates that modulate local plant distributions. For example, two ecologically similar species may exhibit considerable overlap in distribution at the biome or regional scale. But, at the local scale the two species' distributions may overlap very little as competitive interactions could eliminate one or the other on any given substrate or under particular microclimates. Clearly, different processes are operating to produce overlap at one scale and segregation at another. An 'envelope' of constraints (e.g., Fig. 6; O'Neill et al. 1986) will define the region within which two species may coexist. However, the physical mapping of those constraints on a variable landscape (Figs. 5, 6) will determine the length scales of suitable habitats at different places within the region. If topography is complex, the length scales of suitable habitat can become very short and habitat diversity can be quite high, resulting in a segregation of species at local scales.

The overlay of intrinsic spatial and temporal scales of organisms on the climate-induced regional gradients in habitat scale (grain) can modulate the regional expression of species diversity patterns. Given that all regions, even the most topographically homogeneous regions, exhibit some level of substrate variability, the result of these climate-substrate interactions should usually be an increase in beta diversity near biome-scale ecotones. This is manifested by an increase in habitat diversity and a reduction in habitat size. An important exception occurs when organisms alter their phenotypic response to the environment such that the 'perceived' grain size remains large, even near ecotones. It should be emphasized that all levels of constraint, regardless of spatial extent, are physiologically mediated (Cattelino et al. 1979, Neilson 1986, Woodward 1987).

These observations allow some predictive capability of the habitat variability responses to global climatic change. Ecotone location and change

in location could be detectable by monitoring habitat variability patterns through space and time. The consequences of these changes to organisms with different spatial and temporal scaling properties should be amenable to estimation, since abiotic processes appear to be the dominant, ultimate cause of large-scale diversity patterns with increasing importance of biotic interactions as proximate causes of finer scale diversity patterns. Although we have emphasized biome-scale ecotones, the hypotheses should apply to climatically induced ecotones at any scale. The distinctions between the diverse habitat grains near a biome ecotone are, for example, fundamentally microclimatic differences being 'realized' over a variable terrain. Ecotones between these grains should be amenable to the same analysis, targeting even smaller scale organisms (e.g., Rusek 1990). Incorporation of these hypotheses into continental or global scale vegetation models would assist in the assessment of current and potential future risks to biodiversity as a resource.

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FIGURE LEGENDS

1. Biomes of the United States (modified from Dice 1943 and Küchler 1964). The climatic transects are shown (Figs. 2, 3). The hydrologic transect (Fig. 4) closely follows the northern climatic transect.

2. Seasonality of mean total monthly precipitation across the United States along the northern transect (Fig. 1). a) Precipitation (mm/month) is plotted against the months of the year and longitude. The location of the weather stations used to construct the graph are indicated by horizontal lines. Total monthly precipitation data from 1941-1970 were used to calculate the mean values depicted here (Quinlan et al. 1987). b) Contour map of the three dimensional surface. The contour interval is 10 mm. Solid lines to the right of the contour plot indicate the positions of ecotones along the transect, as taken from Fig. 1. CV = California Vegetation, PNW = Pacific Northwest Forests, GBS = Great Basin Sagebrush-Steppe, GBD = Great Basin Desert Scrub, NRM = Northern Rocky Mountain Forests, SRM = Southern Rocky Mountain Forests, SWD = Southwestern Deserts, SGP = Short Grass Prairie, TGP = Tall Grass Prairie, STS = South Texas Savanna, NH = Northern Hardwoods, EDF = Eastern Deciduous Forests, SEF = Southeastern Forests. c) Elevations (m) of the weather stations and of the gauging stations (Fig. 4).

3. Seasonality of precipitation across the southern transect (legends as in Fig. 2).

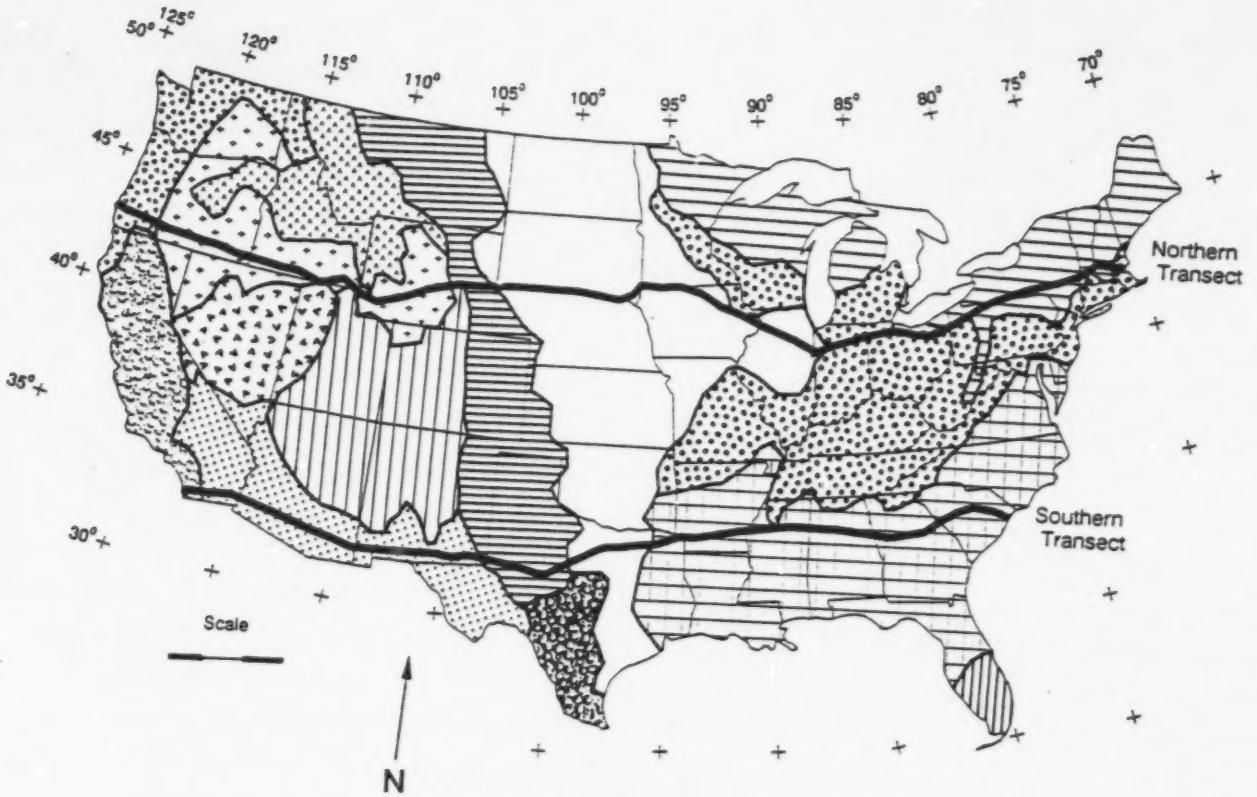
4. Seasonality of monthly runoff across the United States along the northern transect (Figs. 1, 2). a) The vertical axis represents equivalent depth (mm), the horizontal axis represents months of the year, and the diagonal axis represents longitude. The location of the gauging stations used to construct the graph are indicated by horizontal lines. At least 15 years of data were used to calculate the mean values. The runoff data were obtained from the USGS daily stream flow records (US West 1988). b) Contour map of the three dimensional surface. The contour interval is 5 mm. Solid lines to the right of the contour plot indicate the positions of ecotones along the transect, as

taken from Fig 1. See Fig. 2 for key to abbreviations. The elevations (m) of the gauging stations are shown in Fig. 2.

5. Idealized concept of resource availability along an environmental gradient. The abscissa could be scaled to any length units from mm to m to km. The length scale of the abscissa is determined by the physical mapping of the resource gradient in real terrain such that the spatial distribution of the resource is contained within a continuous space. The length scaling of the abscissa should be constrained by regional climatic gradients (see text and Fig. 6). The amplitude of resource availability within a grain can also vary depending on the regional complexity of terrain (see text and Fig. 7).

6. A conceptual model of the regional climatic constraints on the vertical distribution and composition of plant communities along a regional climatic gradient (Neilson and Wullstein 1983, Neilson 1987b). As the gradients converge at the apex of the 'wedge', the size of suitable habitat patches decreases, while their diversity increases (Figs. 6, 7).

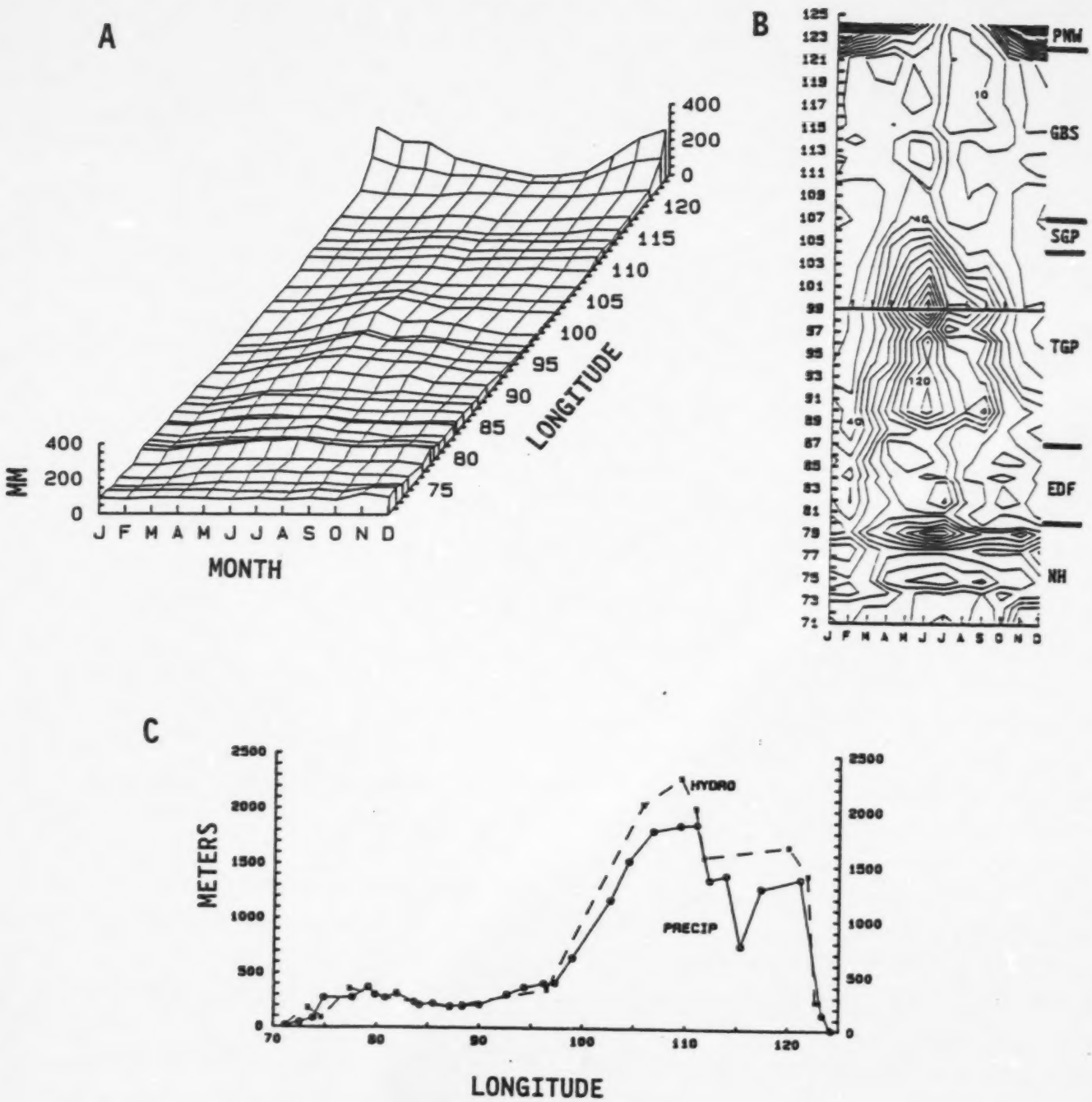
7. The hypothetical diversity of habitats along a transect stretching from one biome to another, across a major ecotone. The diversity of 'perceived' habitats (grains) should increase in complex terrain, but decrease or remain unchanged if there is no substrate complexity. Under complex terrain, the diversity of habitats near the ecotone is obtained by shortening the length scale of the habitat without necessarily changing the amplitude variation of resources within the habitat (Fig. 5). With homogeneous terrain, the length scale of the habitat near the ecotone remains large, while the amplitude of resource variation within the habitat should decrease (Fig. 5).



Biotic Regions

- California Vegetation
- PNW Forests
- Great Basin Sage-Steppe
- Great Basin Desert Scrub
- Northern Rocky Mountain Forests
- Southern Rocky Mountain Forests
- Southwestern Deserts
- Short Grass Prairie
- Tall Grass Prairie
- South Texas Savanna
- Northern Hardwoods
- Eastern Deciduous Forests
- Southeastern Forests
- Subtropical Forests

Figure 1


A
400
200
0
MM
J F M A M J J A S O N D
MONTH
400
200
0
120
115
110
105
100
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90
85
80
75
LONGITUDE
B
PNW
GBS
SGP
TGP
EDF
NH
J F M A M J J A S O N D
C
METERS
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500
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HYDRO
PRECIP
70
80
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120
LONGITUDE

Figure 2

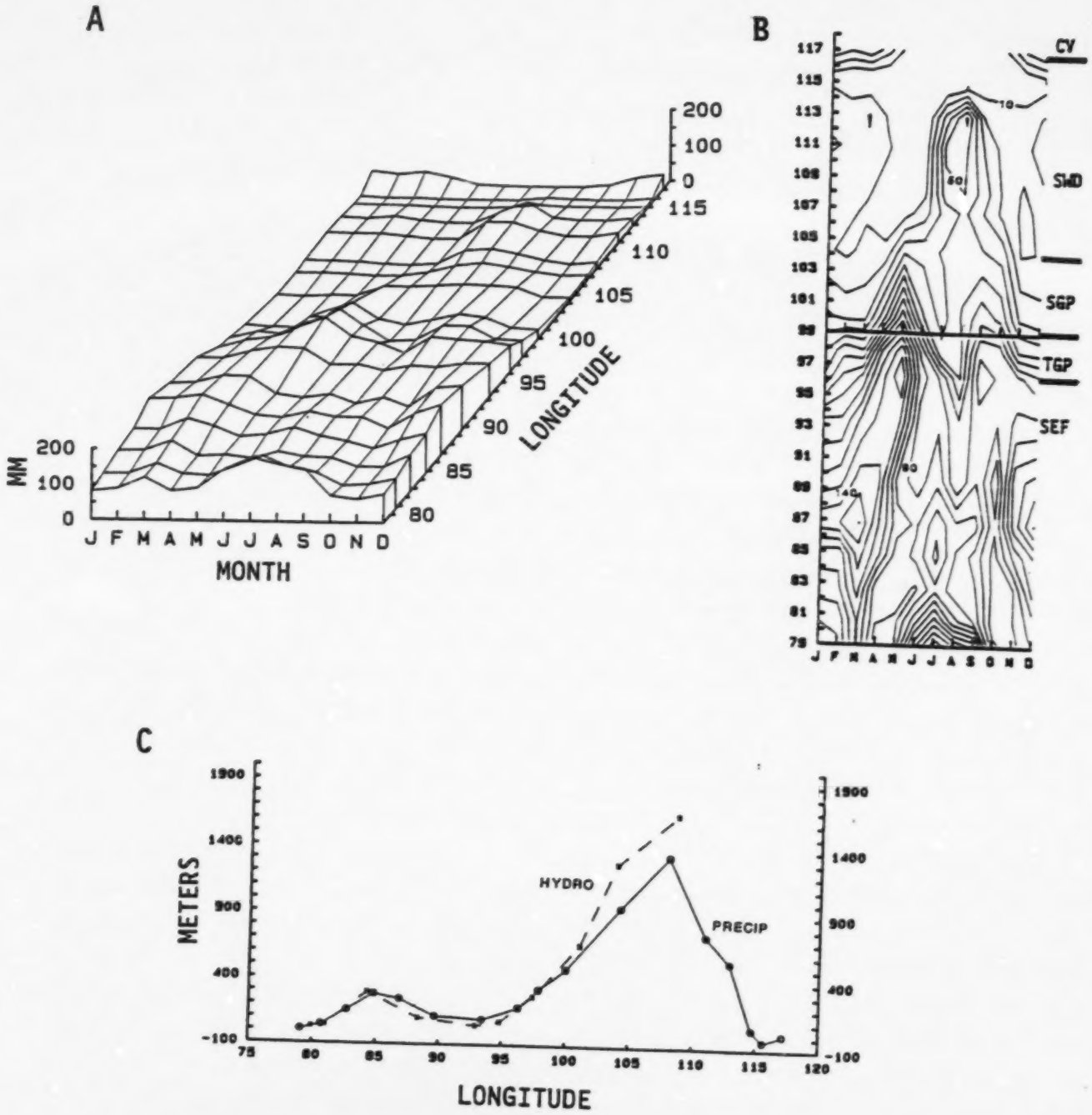
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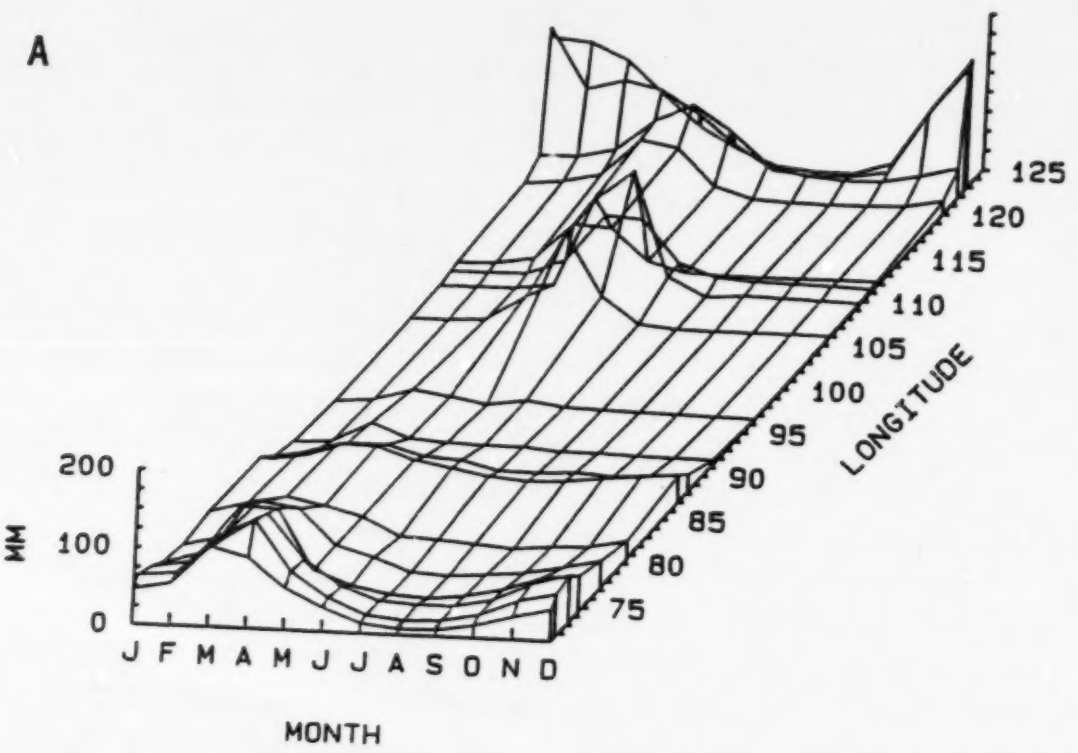
Figure 3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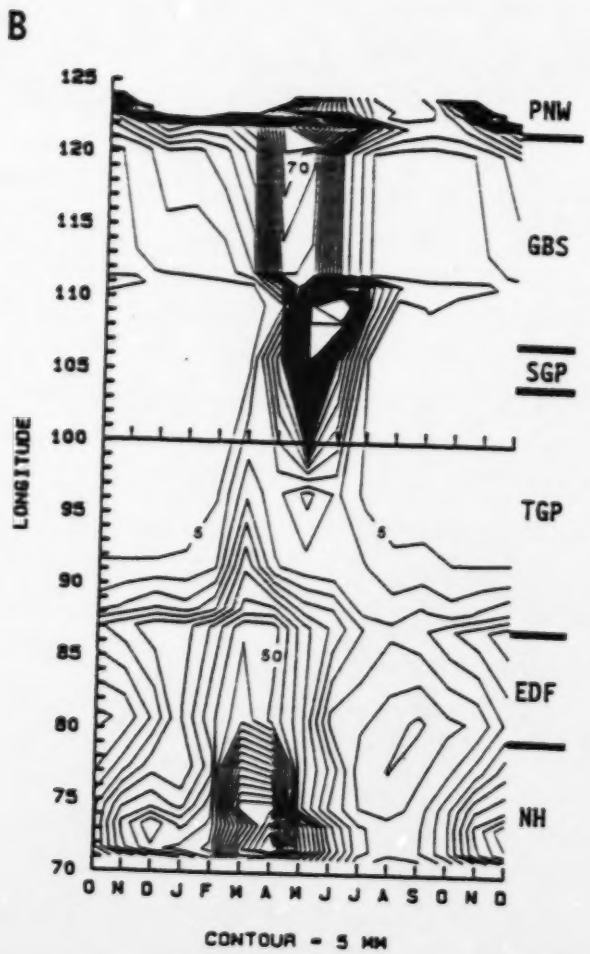
LONGITUDE


B
LONGITUDE
125
120
115
110
105
100
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75
70
O N D J F M A M J J A S O N D
CONTOUR = 5 MM
PNW
GBS
SGP
TGP
EDF
NH
70
5
5
50

Figure 4

Resource Availability
0
10
Resource Gradient (Distance)
(mm, cm, m, or km)

Figure 5

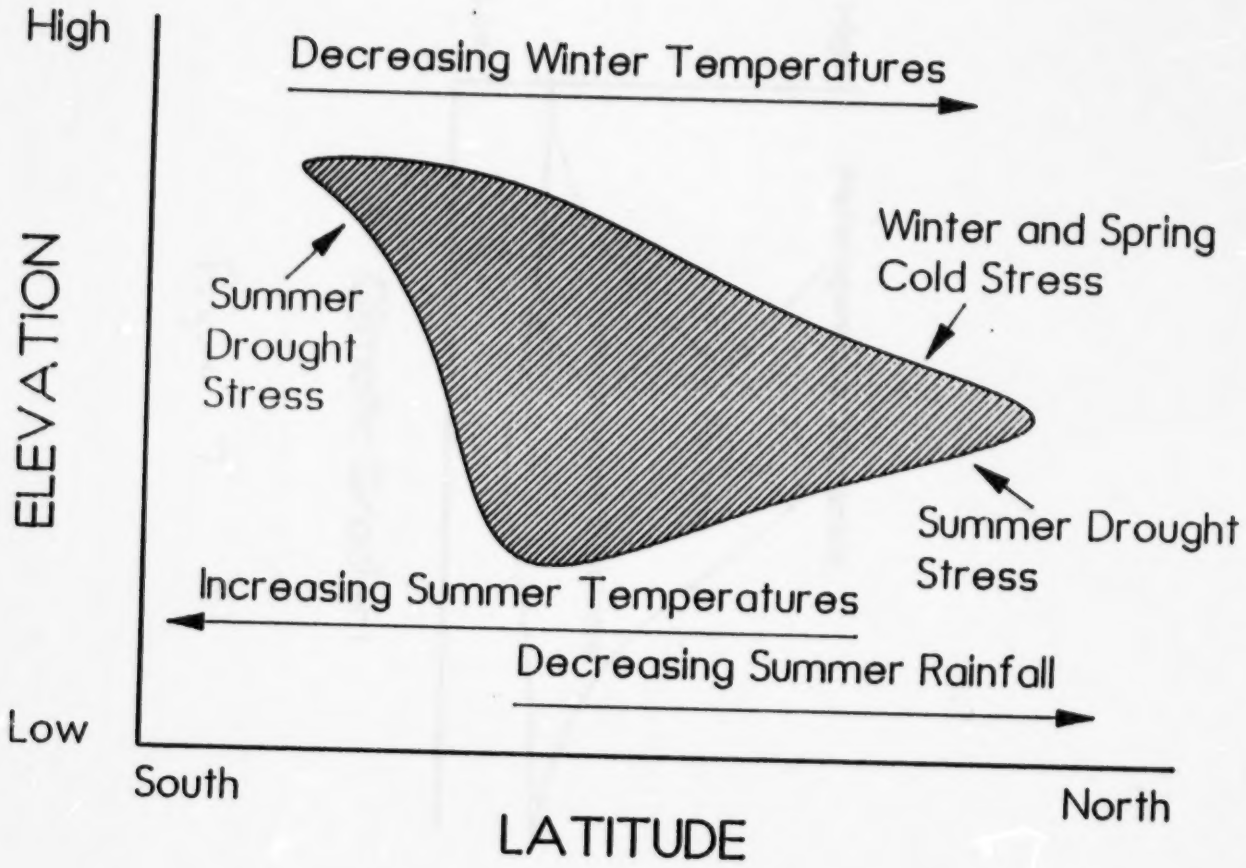
High
Decreasing Winter Temperatures
ELEVATION
Summer
Drought
Stress
Winter and Spring
Cold Stress
Summer Drought
Stress
Increasing Summer Temperatures
Decreasing Summer Rainfall
Low
South
North
LATITUDE

Figure 6

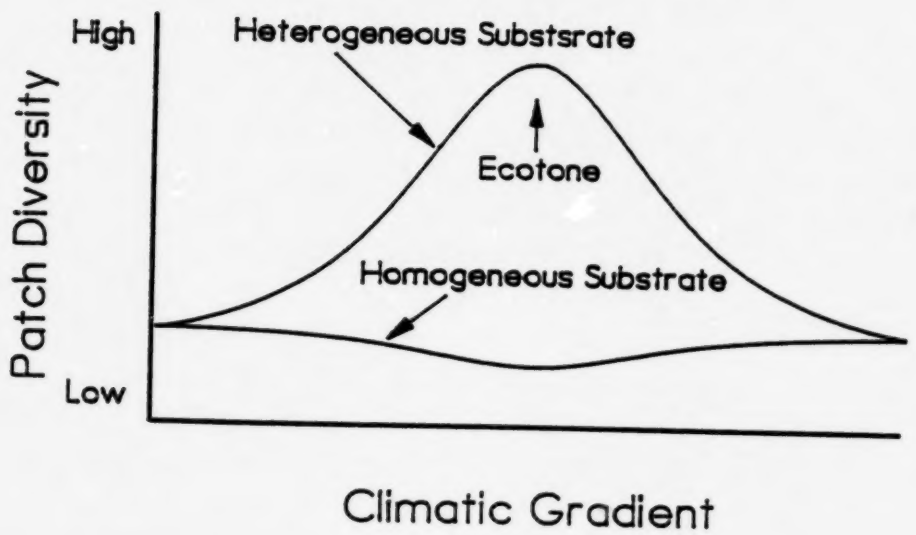
High
Heterogeneous Substsrate
Ecotone
Homogeneous Substrate
Patch Diversity
Low
Climatic Gradient

Figure 7